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Demography of a deep-sea lantern shark (*Etmopterus spinax*) caught in trawl fisheries of the northeastern Atlantic: Application of Leslie matrices with incorporated uncertainties

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Abstract

The deep-sea lantern shark *Etmopterus spinax* occurs in the northeast Atlantic on or near the bottoms of the outer continental shelves and slopes, and is regularly captured as bycatch in deep-water commercial fisheries. Given the lack of knowledge on the impacts of fisheries on this species, a demographic analysis using age-based Leslie matrices was carried out. Given the uncertainties in the mortality estimates and in the available life history parameters, several different scenarios, some incorporating stochasticity in the life history parameters (using Monte Carlo simulation), were analyzed. If only natural mortality were considered, even after introducing uncertainties in all parameters, the estimated population growth rate (λ) suggested an increasing population. However, if fishing mortality from trawl fisheries is considered, the estimates of λ either indicated increasing or declining populations. In these latter cases, the uncertainties in the species reproductive cycle seemed to be particularly relevant, as a two-year reproductive cycle indicated a stable population, while a longer (three-year cycle) indicated a declining population. The estimated matrix elasticities were in general higher for the survivorship parameters of the younger age classes and tended to decrease for the older ages. This highlights the susceptibility of this deep-sea squaloid to increasing fishing mortality, emphasizing that even though this is a small-sized species, it shows population dynamics patterns more typical of the larger-sized and in general more vulnerable species.

Keywords: Bottom trawling, deep-sea sharks; deep-sea fisheries; demographic analysis, fishing mortality; population dynamics.

1. Introduction

Elasmobranch fishes are generally considered to be highly vulnerable to fishing mortality, mainly because of their life history characteristics that include slow growth rates, late maturities and low fecundities (Cortés, 2000; Hoenig and Gruber, 1990). Overexploitation in these animals may occur even with relatively low levels of fishing mortality (Stevens et al., 2000). Deep water elasmobranchs seem to be even less resilient to fishing mortality than most of the coastal species (Gordon, 1999), and are currently amongst the groups that present the highest risks of population declines (Fowler et al., 2005).

In Portuguese waters, relatively large quantities of deep-sea velvet belly lantern sharks, *Etmopterus spinax*, are commonly caught as bycatch in trawl fisheries targeting mainly deep water crustaceans (Borges et al., 2001; Monteiro et al., 2001). Most of this bycatch is discarded due to the very low commercial value of this species, making it very difficult to gather information on the impact of these commercial fisheries on these shark populations (Coelho and Erzini, 2008a). *Etmopterus spinax* occurs in deep waters, on or near the bottoms of the outer continental shelves and slopes, and is distributed along the north and central eastern Atlantic Ocean, including the Mediterranean Sea (Compagno et al., 2005). In the northeast Atlantic, some previous studies have focused on the life history parameters of this species, including the works of Coelho and Erzini (2005) and Coelho and Erzini (2008b) on the age, growth and reproductive parameters, and Neiva et al. (2006) on the feeding ecology.

Mortality rates are some of the most important parameters for fisheries biology and stock assessment studies (Maunder and Wong, 2011; Vetter, 1988). Although several approaches have been developed to estimate mortality rates, they still are some of the most difficult and uncertain parameters to estimate (Cortés, 2007). Understanding mortality is very important because of the need to know how fast individuals are removed from the population in order to model the population dynamics and to estimate sustainable rates of exploitation (Simpfendorfer et al., 2004). Demographic analysis is useful to determine the potential for decline in a population and to diagnose population susceptibility to fishing pressure (Simpfendorfer, 2004), and is well suited for data deficient species due to the requirement of few parameters (mainly biological), as opposed to other stock assessment methods that rely mainly on fisheries data.

Demographic analysis based mainly on life history parameters has become widely used for modeling elasmobranchs (e.g. Aires-da-Silva and Gallucci, 2007; Cortés and Parsons, 1996; Romine et al., 2009). However, most of the studies have focused primarily on species and populations of commercially important coastal and pelagic elasmobranchs, but very little is currently known about the less valuable species that are caught as bycatch and usually discarded, such as the lantern sharks of the family Etmopteridae. Although some previous studies have focused on the life history parameters of *E. spinax* in the northeast Atlantic, the question of how much the commercial fisheries are impacting the populations remains unanswered. Therefore, the objectives of the present study were to: 1) estimate mortality and survivorship parameters for *E. spinax*; 2) develop age-specific demographic models; 3) consider different possible scenarios in terms of survivorship and life history parameters and 4) evaluate the effects of introducing uncertainty in the analysis.

2. Material and Methods

2.1. *Life history parameters*

Life history parameters including age and growth estimates, size-at-age data, maximum age, and age at 50% maturity for the deep-sea lantern shark *E. spinax* in the northeast Atlantic have been previously studied and are available from the literature (Coelho and Erzini, 2008b) (Table 1). With regards to fecundity parameters, Coelho and Erzini (2008b) presented a significant relationship between female size and fecundity, and given the correlation between size and age, it is expected that a similar relationship is also significant between female age and fecundity. In this study, an age-oocyte relationship was investigated by linear regression analysis, and used to estimate age-specific fertilities for the species.

For the demographic analysis, the age-specific fertility was converted into female pup natality by multiplying the estimated fertility-at-age by 0.5 (assumed as the proportion of female embryos in each litter). This value was then divided either by 2 or 3, depending on the assumption of a 2 or a 3 year reproductive cycle for this species (Coelho and Erzini, 2008b), a parameter still uncertain, but considered in the different scenarios assumed in this paper.

2.2. *Estimating mortality and survivorship*

Mortality was estimated both by indirect empirical techniques (M , natural mortality) that use equations to correlate different life history parameters with mortality, and by catch curve analysis (Z , total mortality) (Simpfendorfer et al., 2004).

The indirect estimates included age-independent equations such as the equations proposed by Pauly (1980) using the L_{inf} (maximum asymptotic species size) and k (growth coefficient) parameters from the von Bertalanffy growth function (VBGF), the Hoenig (1983) equation developed for teleosts and using maximum observed ages, and the two Jensen (1996) equations using age at maturity and k from the VBGF.

Pauly (1980) equation:

$$\log M = -0.066 - 0.279 \log L_{inf} + 0.6543 \log K + 0.4634 \log T,$$

where M is natural mortality, L_{inf} and k are VBGF parameters and T is the average water temperature. In this case, water temperature was considered to be 13.0°C, based on CTD (conductivity, temperature and depth) recordings during 15 commercial bottom trawl sets (210 data points) carried out while collecting the specimens for the biological studies.

Hoenig (1983) equation:

$$\ln(Z) = 1.46 - 1.01 \ln(t_{max}),$$

where Z is total mortality and t_{max} is the maximum observed age.

The two Jensen (1996) equations, one based on age at maturity and the other on the VBGF parameters:

$$M = \frac{1.65}{X_m},$$

$$M = 1.5K,$$

where M is natural mortality, X_m is age at first maturity and k is the growth coefficient from the VBGF.

Additionally, indirect methods using age-dependent equations were also used, including the Peterson and Wroblewski (1984) equation that estimates natural mortality as a function of weight at age, and the Chen and Watanabe (1989) equations that use VBGF parameters to calculate age-specific mortality $M(t)$. Chen and Watanabe (1989) hypothesized that natural mortality in fish populations should have a U-shaped (bathtub) curve when plotted against age, and therefore proposed two equations: one describing falling mortality rates in early life stages/ages, and a second describing the increasing mortality towards later life stages/ages.

Peterson and Wroblewski (1984) equation:

$$M_w = 1.92w^{-0.25},$$

where M_w is the natural mortality for a given dry weight (w) organism. Dry weight was obtained from total weight and considering the conversion factor of 1/5 proposed by Cortés (2002) for elasmobranchs.

Chen and Watanabe (1989) equations for younger and older life stages (with t_m being the age at first maturity):

$$M(t) = \begin{cases} \frac{K}{1 - e^{-k(t-t_0)}}, t \leq t_m \\ \frac{K}{a_0 + a_1(t-t_m) + a_2(t-t_m)^2}, t \geq t_m \end{cases},$$

where

$$\begin{cases} a_0 = 1 - e^{-K(t_M - t_0)} \\ a_1 = K e^{-K(t_M - t_0)} \\ a_2 = -\frac{1}{2} K^2 e^{-K(t_M - t_0)} \end{cases},$$

and

$$t_M = -\frac{1}{K} \ln(1 - e^{K t_0}) + t_0.$$

Total mortality (Z) was also estimated based on age-structured catch curve analysis (Simpfendorfer et al., 2004). In this analysis, the logarithm of the catch in number of specimens (n) by age class was plotted, and a linear regression was fitted to the descending part of the plot. The initial age classes (ascending part of the curve) were not used in the linear regression as they were assumed to correspond to age classes not yet fully recruited to the fishery. This analysis was carried out using trawl fisheries catch data, given that trawl is the main fishery capturing this species in the region (Coelho and Erzini, 2008a). To reduce the relative impact of the older age classes (with fewer individuals), the weighted regression methodology as suggested by Maceina

and Bettoli (1998) was used. The analysis was run for each sex separately, as well as for sexes combined.

Both the M estimated from the indirect empirical equations and the Z estimated from the catch curve analysis were transformed into annual probabilities of survival (S), as used for example by Hisano et al. (2011), using the equations:

$$S = e^{-Z} \quad \text{or} \quad S = e^{-M}.$$

2.3. Demographic model

Demographic analysis was carried out using age-structured Leslie matrices (Caswell, 2001). Since only females produce offspring, the demographic analysis was carried out exclusively for the female component of the population (Simpfendorfer, 2004). The age-structured model conceived was a pre-breeding survey model, where reproduction and natality take place first, followed by the probability of survivorship-at-age. Thus the age-specific fecundity values of the Leslie matrix were calculated as the products of the age-specific fertilities (m_x) and the first year survivorship (s_0): $F_x = s_0 \cdot m_x$. Additionally, the age-specific probability of being mature (p_{mat} , estimated from the maturity ogives presented by Coelho and Erzini, 2008b) was also considered and used to correct those age-specific fertilities: $F_{x,corrected} = F_x \cdot p_{mat}$. In terms of survivorship, when the age-specific survivorship was estimated from the natural mortality the values were used directly, while when the total mortality was considered (estimated from the catch curves) those values were only used for the ages fully recruited to the fishery (ages 2 and older), while for the younger ages only the natural mortality was considered.

The parameters estimated and analyzed with the demographic analysis were the population finite growth rate (λ), the stable age-distribution vector (w), the age-specific reproductive value vector (v), and the elasticities of the matrix elements (e_{ij}). Within this matrix formulation, λ was calculated as the dominant eigenvalue of the projection matrix. The vectors of the stable age distribution (w) and the age-specific reproductive value (v) were given by the dominant right and left eigenvectors, respectively. The elasticities of each matrix element (e_{ij}) were calculated according to Caswell (2001) by:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{w \cdot v},$$

where a_{ij} is the matrix element corresponding to row i and column j , v_i is the value of row i in the reproductive value vector v , w_j is the value of column j in the stable age distribution vector w , and $\langle w, v \rangle$ is the scalar product of vectors w and v . Elasticities represent a measure of the relative contribution of each matrix element to the value of λ , with the sum of all the matrix elements elasticities equaling 1.

2.4. Incorporating uncertainty

Several different scenarios were considered to be analyzed and compared with the Leslie matrices (Table 2). These scenarios accounted for different possible alternatives that can be used to estimate survivorship (empirical equations vs. catch curves), and fecundity (either a 2 or 3-year reproductive cycle, still uncertain for the species).

Considering that the two input parameters used in the matrices (age-specific fecundity and survivorship) are estimates that have associated uncertainties, it is important to also consider the

uncertainty in the analysis, and in particular how that uncertainty will impact the results of the analysis. Therefore, besides the deterministic scenarios that considered only point estimates as input parameters, some scenarios with associated stochasticity in the life history parameters were also considered (Table 2). A combination of deterministic scenarios (using minimum and maximum values from the survivorship empirical equations, and point estimates from the catch curves and age-specific fertilities) and stochastic scenarios (using values randomly selected from distributions) were considered in the analysis (Table 2).

For incorporating stochasticity in the survivorship parameters, two types of distributions were considered depending on the survivorship estimation method. When survivorship was estimated from the indirect empirical methods, uncertainty was introduced by generating age-specific random survivorship values from a uniform distribution with support defined between the minimum and maximum empirical age-specific estimates. When survivorship was estimated from the catch-curves, uncertainty was introduced by generating random survivorship values from a normal distribution with parameters estimated from the catch curve parameters (point estimate and standard deviation of the catch regression curves). For the fecundity parameters, uncertainty was considered by generating random age-specific fertilities based on a normal distribution, with the expected values and standard deviations based on the fertility-at-age values. Each stochastic scenario was simulated using 10,000 Monte Carlo replicates varying each input parameter based on the previously assumed distributions. The resulting 10,000 Leslie matrices were analyzed, and the distributions of the output parameters were summarized and interpreted in terms of their mean and corresponding 95% confidence intervals (0.025 and 0.975 quantiles).

To conduct matrix analysis computations we used the open-source statistical software R project version 2.14.0 (R Development Core Team, 2011). Some functions were installed from libraries *primer* (Stevens, 2009), *popbio* (Stubben and Milligan, 2007), *FSA* (Ogle, 2011), *reshape* (Wickham, 2007) and *ggplot2* (Wickham, 2009).

3. Results

3.1. Age-specific fecundity and survivorship

A significant relationship between the number of oocytes and female age was established (ANOVA table: $F=33.2$, $p < 0.001$), with the expected number of oocytes increasing 1.26 times ($SE = 0.22$) per each increasing year in the age of the females (Figure 1).

Different mortality (or survivorship) values were obtained depending on the indirect method (equation) used. The specific survivorship values obtained with each empirical equation, as well as age-specific minimum and maximum estimates are summarized in Table 3.

Given that age-structured catch data was available for trawl fisheries, an age-structured catch curve analysis was also performed, with the catch curve plots presented in Figure 2. The estimated Z values were 0.414 for females and 0.546 for males, corresponding to estimated survivorship values of 0.661 ($SE=0.071$) for females and 0.579 ($SE=0.115$) for males. Even though the males had slightly higher total instantaneous mortality rates, corresponding to lower survivorships, the 95% confidence intervals were overlapped and therefore the differences between the two sexes were not significant.

3.2. *Finite rate of population increase (λ)*

The outputs of the estimated rates of population increase (λ) in each of the scenarios considered are summarized in Figure 3. It is interesting to note that when considering only natural mortality from the empirical equations (scenarios 1, 2 and 3) the values of λ were higher than 1 (only slightly in scenario 2), suggesting an increasing population if no fishing mortality was considered. The particular case of scenario 4 produced a value of λ lower than 1, with that scenario corresponding to the worst case scenario, i.e. the species having a three-year reproductive cycle and always considering the minimum survivorship from the empirical equations (corresponding to the maximum natural mortality estimates).

In these deterministic cases, if a three-year reproductive cycle and minimum (empirical) or catch-curve survivorship is considered, then the population would decrease; if a two-year reproductive cycle and minimum (empirical) or catch-curve survivorship is considered, then the population would be nearly stable (or slightly increasing). However, when maximum (empirical) survivorship is considered, the population would increase, regardless of the reproductive cycle.

By adding uncertainty to the analysis, but still using survivorship from the empirical mortality equations (scenarios 7 and 8), the corresponding 95% CI of λ were always higher than 1, meaning that even with uncertainty in the estimation of survivorship and fecundity the population would be increasing when considering only natural mortality from the indirect equations (Figure 3).

In the scenarios considering total mortality from the trawl fisheries catch curves (scenarios 5, 6, 9 and 10) the point estimates of λ were slightly higher than 1 when assuming a two-year reproductive cycle (scenarios 5 and 9), and lower than 1 when assuming a three-year cycle

(scenarios 6 and 10). The confidence intervals of the stochastic scenarios (9 and 10) included the value of 1 (with very little probability in scenario 10), suggesting that even when accounting for the trawl fishing mortality, and independent of the reproductive cycle (two or three years), this population could be varying very slowly in time or possibly in a stable condition (Figure 4).

3.3. Stable age distribution (w) and reproductive value (v)

The stable age distributions vectors (w) given by the dominant right matrix eigenvectors across the 10 different scenarios considered were very similar, while the age-specific reproductive values given by the dominant left eigenvectors varied more depending on each scenario considered (Figure 5). Still, for all scenarios considered, the reproductive values tended to increase until age 5, followed by a peak between ages 6 and 8, and then decreased until the maximum observed age of 11 years for the species (Figure 5).

3.4. Matrix elasticities (e_{ij})

The relative matrix elasticity values for the reproductive parameters were substantially lower than the elasticities for the survivorship parameters (Figure 6). With regards to the survivorship parameters the elasticities were higher for the younger age classes and tended to decrease for the older ages. For the fecundities, the higher values were obtained for age-class 6 (for all scenarios), and tended to decrease progressively for both the younger and older age classes (Figure 6).

4. Discussion

One of the most important parameters of interest in demographic analysis is the finite rate of population increase (λ). In this study, we simulated different scenarios, and it is particularly important to consider the estimated λ in each scenario. In the scenarios considering only natural mortalities from empirical equations, the λ values tended to be larger than 1, suggesting that in those cases the population would be increasing. Even when uncertainty was incorporated (by allowing survivorship and fertilities to be randomly selected between a range of possible values), the λ values, including their 95% confidence intervals, tended to be larger than 1. On the other hand, when fishing mortality from trawl fisheries (estimated with catch curves) was considered, the λ values could either be higher or lower than 1, usually depending on the assumed reproductive cycle (two or three year cycle), suggesting that in such cases this parameter plays a very important role.

In terms of species comparisons, previous λ values estimated for elasmobranchs are highly variable, ranging from species that in optimal conditions can increase around 50% per year (e.g. $\lambda=1.6$ for the scalloped hammerhead (*Sphyrna lewini*) and $\lambda=1.4$ for the blue shark (*Prionace glauca*)), to cases of species having negative λ values, such as the piked dogfish (*Squalus acanthias*) and the blacknose shark (*Carcharhinus acronotus*) (Cortés, 2002). In this way, the lantern shark (*Etmopterus spinax*) in the present study seems to be more similar to the species with lower values of λ , with some scenarios also producing rates of population increase very close to 1, even when considering only natural mortality rates.

Elasticities are other important values that can be extracted from this analysis and that may be particularly important for fisheries management and conservation purposes. Major efforts should focus on the matrix elements (stages or ages) with highest elasticities, as those will produce the largest changes in the population growth rates. In this particular case, and for all scenarios that were considered in the analysis, it seems that the age classes with higher elasticities are the age classes corresponding to the juvenile stages, mainly between ages 1-4, with higher elasticities in the survivorship parameters rather than in the fecundity parameters. This means that any future conservation or management initiatives for this species should focus on increasing the survivorship of these juvenile age classes.

Previous comparisons of the elasticities of smaller sized and faster growing elasmobranchs with those of larger and generally slower growing species has shown that the elasticities of the smaller and faster growing species tend to be equally distributed between juvenile and adult stages, and that in those cases the fecundity elasticities also tend to be relatively higher (Cortes, 2002). On the other extreme, Cortés (2002) also noted that the larger sized and slower growing species tend to have higher elasticities in the juvenile stages, and lower elasticities for the adults and for the fecundity parameters. Therefore, and even though *E. spinax* is a small sized species, it seems to fall within the elasticities expected for the larger and slower growing species. This exception for Squaliformes and other deep-sea sharks has been previously noted by Cortés (2002), specifically for the shortspine spurdog (*Squalus mitsukurii*) and the piked dogfish (*S. acanthias*), that are also relatively small sized sharks, but show elasticities more typical of the larger species. The results presented in the present study seem to confirm that even though many deep-sea Squaliformes sharks are general small sized species, their population dynamics are relatively more similar to

those of the larger species, and should therefore be managed in a similar way to those larger and slower growing species.

Our demographic analysis with matrix models should be interpreted with caution as it relies on some restricted assumptions. One possible shortcoming of this approach is that density-dependence is usually not considered, but it is possible and even expected that life history parameters will change over time as a function of population size or density. However, by incorporating stochasticity in some of our analyzed scenarios, the results presented herein already take into account, to some degree, possible changes in those parameters over time. Another limitation of the analysis is the fact that eventual auto-correlation in the matrix parameters was not considered, and that should be tested in the future, for example by generating auto-correlated parameters for the matrices. Finally, the random distributions in the life history parameters for the stochastic scenarios come from some form of known distributions, and in our study we assumed a normal distribution for the fecundity parameters, and either a uniform or a normal distribution for the survivorship parameters (depending on the method used to estimate the mortality). However, future analysis may consider and test alternative distributions, such as the beta distribution for the survivorship parameters and the lognormal for the reproductive parameters. Another possible source of bias may be related to the empirical estimations of natural mortality based on life history parameters, given that the biological data was collected from a population with a long history of fishing pressure. In this case, the empirical mortality estimations may be closer to the total mortality rather than to the natural mortality of the population. Despite all the possible limitations, demographic analysis based mainly on life history parameters seems to be a very good approach to analyzing population dynamics of data-poor species, such as most elasmobranchs (Simpfendorfer, 2004), and in particular *E. spinax*.

Other studies that have used similar techniques for analyzing population dynamics in elasmobranchs include Aires-da-Silva and Gallucci (2007) for blue shark in the North Atlantic, and Cortés (1999) for the sandbar shark (*Carcharhinus plumbeus*) in the U.S. Atlantic and Gulf of Mexico, in this case using a stage-based matrix rather than an age-based approach. Other approaches to demographic analysis utilize life tables rather than Leslie matrices (Simpfendorfer, 2004). This approach has been used in the past for elasmobranch fishes including Cailliet (1992) for the leopard shark (*Triakis semifasciata*) in California, Cortés (1995) for the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) in the Gulf of Mexico, Marquez-Farias and Castillo-Geniz (1998) also for *R. terraenovae* but in the southern Gulf of Mexico, Cortés and Parsons (1996) for the bonnethead (*Sphyrna tiburo*) in the Gulf of Mexico, and Romine et al. (2009) for the dusky shark (*Carcharhinus obscurus*) in the northwest Atlantic. Mollet and Cailliet (2002) compared life tables, Leslie matrices and stage-based matrices (with different stage durations) and concluded that the results from life tables and Leslie matrices were similar, while the stage-based models (particularly matrices with few stages) had different dynamics with shorter recoveries to the stable age distribution. According to Mollet and Cailliet (2002), stage-based models with few stages tended to underestimate elasticities of juvenile survivorship and overestimate survivorship elasticities of the adults.

Regardless of the chosen approach (life table, age-structured Leslie matrix or stage-based approaches), it is important to account for uncertainty in the input parameters in the models (Cortés, 2002). Demographic analysis is based mainly on two parameters, the fecundity and survivorship from one age or stage to the next age or stage. While the reproductive parameters can typically be estimated relatively easily from life history parameters (except usually the reproductive periodicity), the survivorship parameters are generally more complex to estimate

and are usually based on several assumptions. Different approaches can be used to estimate survivorship, ranging from empirical approaches based on life history parameters, to catch curve approaches based on total mortality from the fisheries. Therefore, it is important to account for these sources of uncertainty in the analysis, and study not only the point estimate of the parameter but also the confidence intervals that can reflect and account for this uncertainty. This was accomplished in the present study by using Monte Carlo simulations to account for the uncertainties in the input survival and fecundity parameters in the Leslie matrices.

In this paper we analyzed the demography of a poorly known and studied deep-sea shark captured as bycatch and impacted by commercial deep-sea trawl fisheries in the northeast Atlantic. Given the uncertainty in the species' life history parameters, simulations with stochastic scenarios were carried out, with those considered to reflect the best estimates of the demographic parameters for this deep-sea shark. When only the natural mortality was considered the species showed positive rates of population increase, but by adding fishing mortality to the models the species seems to be either in a stable condition or possibly declining. Such uncertainties are mainly related to stochastic variations in terms of the life history parameters, and hence the importance of such baseline studies for determining the status of the populations. Even though *E. spinax* is a small sized deep-sea shark, the elasticities showed patterns more typical of the larger sized and slower growing species, emphasizing the vulnerability of this group of fishes (deep-sea squaloids) to increasing fishing mortality.

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Figure captions

Figure 1: Relationship between the number of oocytes and age for adult *Etmopterus spinax* females. The linear regression is shown as the solid black line and the 95% confidence intervals as the dotted lines.

Figure 2: Age structured catch curve analysis for *Etmopterus spinax* captured as bycatch in trawl fisheries in the northeast Atlantic, for A) sexes combined; B) females; and C) males. The solid black line in each plot represents the weighted linear regression fitted to the fully recruited age classes (full circles) representing Z , the instantaneous total mortality rates.

Figure 3: Estimates of λ (lambda, finite rate of population increase) under the various scenarios considered in the study. The black circles represent the point estimates, and the vertical lines represent the 95% confidence intervals estimated with Monte Carlo simulation in the stochastic scenarios.

Figure 4: Variability in the estimates of λ (lambda, finite rate of population increase) in the demographic scenarios that include uncertainties in the life history input parameters. Each model was run 10,000 times by Monte Carlo simulation and the histograms represent the frequency of occurrence (in density) of the estimated λ . The 95% confidence intervals (0.025 and 0.975 quantiles) are represented as vertical dotted lines in the plots.

Figure 5: A) Stable age (w) and B) reproductive value (v) distributions of the *Etmopterus spinax* age classes, considering the various scenarios described in Table 2. **(NOTE: The color version of this Figure is intended for color reproduction on the Web only, and a black-and-white version is submitted for the printed version of the paper).**

Figure 6: Values of matrix elasticities for each of the scenarios described in Table 2. The diagonals represent the elasticities for the survival-at-age and the first row represents the elasticities for the age-specific fecundities. The figures are coded in color, with darker colors corresponding to matrix elements with higher elasticities and lighter colors corresponding to matrix elements with lower elasticities. Matrix elements that do not occur have a value of zero and are represented in white. *(NOTE: The color version of this Figure is intended for color reproduction on the Web only, and a black-and-white version is submitted for the printed version of the paper).*

Tables

Table 1: Life history parameters previously published for *Etmopterus spinax* in the northeast Atlantic (data from Coelho and Erzini, 2008b), and used for estimating mortality and survivorship parameters used in the demographic analysis. Both the point estimates and the standard deviations (SD) are presented. In the TL-W relationship, a represents the intercept and b the coefficient of the regression.

	Parameter	Estimate	SD
Age & growth	L_{inf} (cm)	55.8	5.94
	k (year ⁻¹)	0.12	0.02
	t_0 (year)	-1.99	0.18
	Max. age (years)	11	-
Reproduction	Age at 50% maturity (years)	4.7	0.05
	Fecundity	9.94	2.61
	Periodicity	2-3 years	-
TL-W relationship	a	0.002	0.06
	b	3.29	0.02

Table 2: Scenarios considered in this study, with varying underlying conditions assumed for the estimates of age-specific survivorship and fecundity. For the reproduction parameters, the method used was a regression analysis. The uncertainty regarding the periodicity of the reproductive cycle (2 or 3 year cycle) was also considered in the scenarios analyzed.

Type	Scenario	Survivorship		Reproduction		Model assumptions
		Method	Estimate	Cycle (years)	Estimate	
Deterministic	1	Empirical	Max	2	Point est	2 year cycle, max empirical survivorship
	2	Empirical	Min	2	Point est	2 year cycle, min empirical survivorship
	3	Empirical	Max	3	Point est	3 year cycle, max empirical survivorship
	4	Empirical	Min	3	Point est	3 year cycle, min empirical survivorship
	5	Catch-curve	Point est.	2	Point est	2 year cycle, catch-curve survivorship
	6	Catch-curve	Point est.	3	Point est	3 year cycle, catch-curve survivorship
Stochastic	7	Empirical	uniform	2	normal	2 year cycle, random empirical survivorship and random fecundity
	8	Empirical	uniform	3	normal	3 year cycle, random empirical survivorship and random fecundity
	9	Catch-curve	normal	2	normal	2 year cycle, random survivorship from catch curve and random fecundity
	10	Catch-curve	normal	3	normal	3 year cycle, random survivorship from catch curve and random fecundity

Table 3: Survivorship of *Etmopterus spinax* estimated with indirect age-dependent and age-independent methods based on life history parameters, and estimated from the catch-curve analysis. In the catch curves, only the mortalities for the ages fully recruited to the fishery (ages 2 and older) were considered, and not estimated (NA) for the younger ages.

Age	Age-dependent methods		Age-independent methods				Catch-curve analysis
	Peterson & Wroblewski (1984)	Chen & Watanabe (1989)	Hoenig (1983)	Pauly (1980)	Jensen (1996) t_{mat}	Jensen (1996) k	
0	0.714	0.568					NA
1	0.776	0.672					NA
2	0.811	0.729	0.682	0.769	0.704	0.835	0.661
3	0.834	0.766	Same values for all ages				
4	0.849	0.791					
5	0.860	0.839					
6	0.869	0.844					
7	0.876	0.848					
8	0.881	0.851					
9	0.885	0.854					
10	0.889	0.857					
11	0.892	0.857					

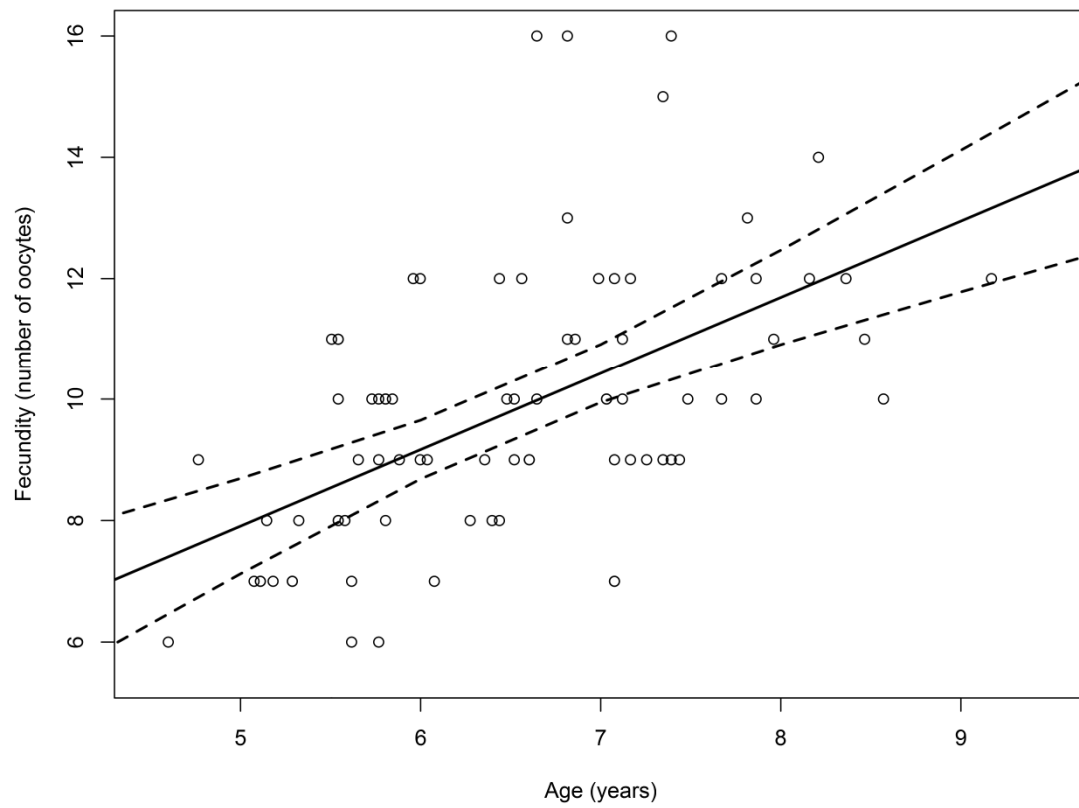
Figures

Figure 1.

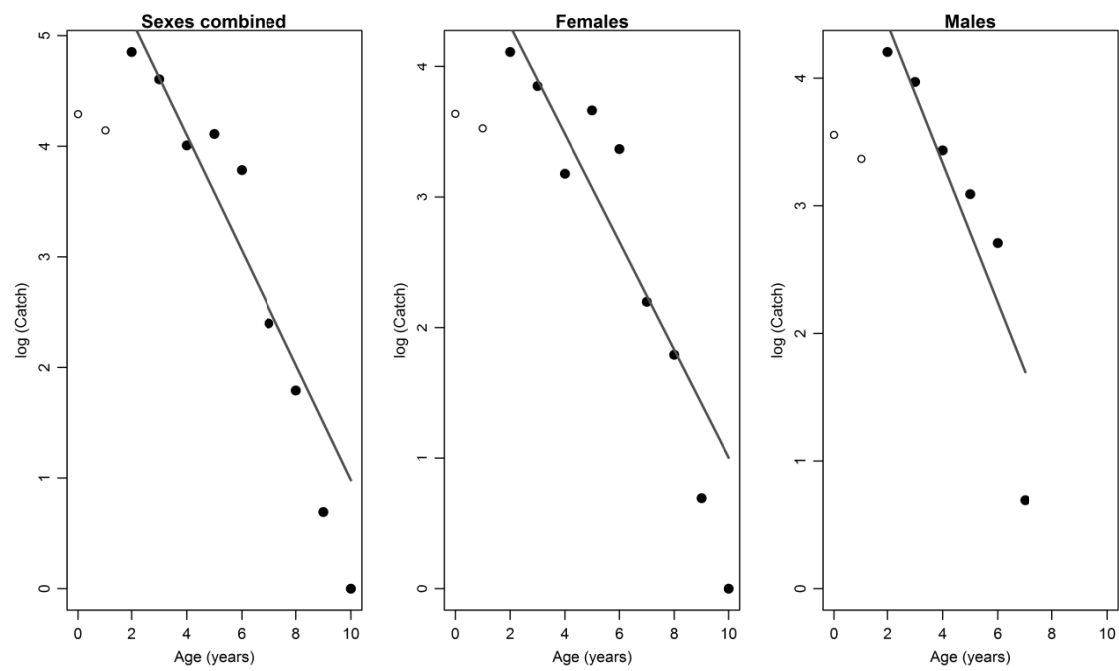


Figure 2

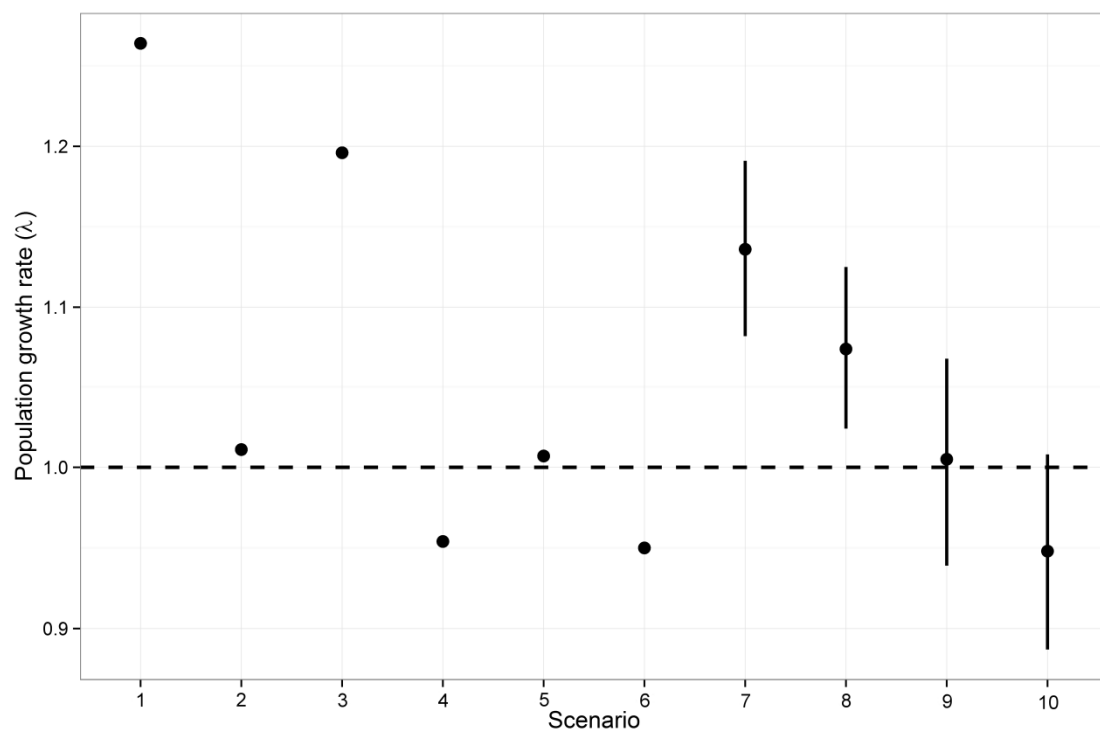


Figure 3.

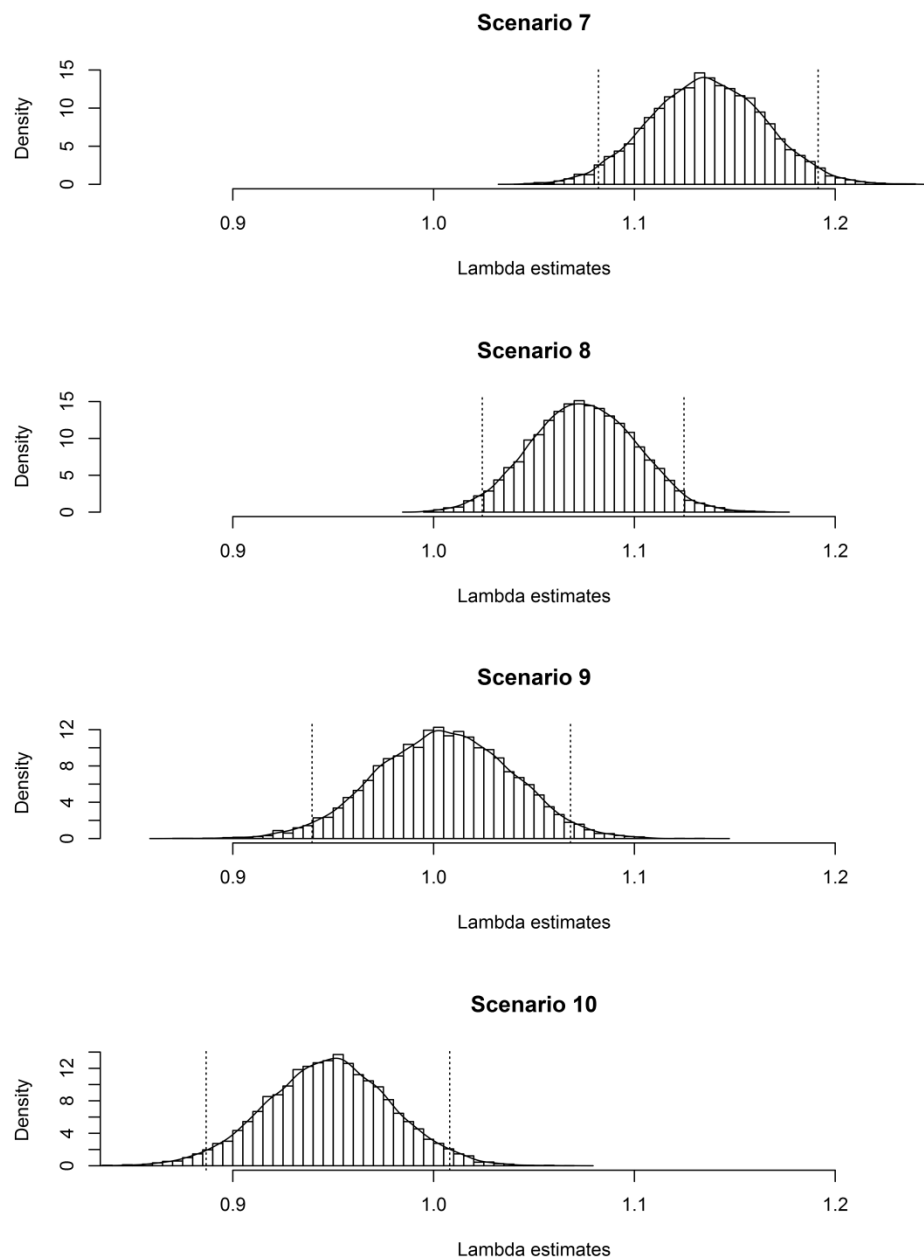


Figure 4.

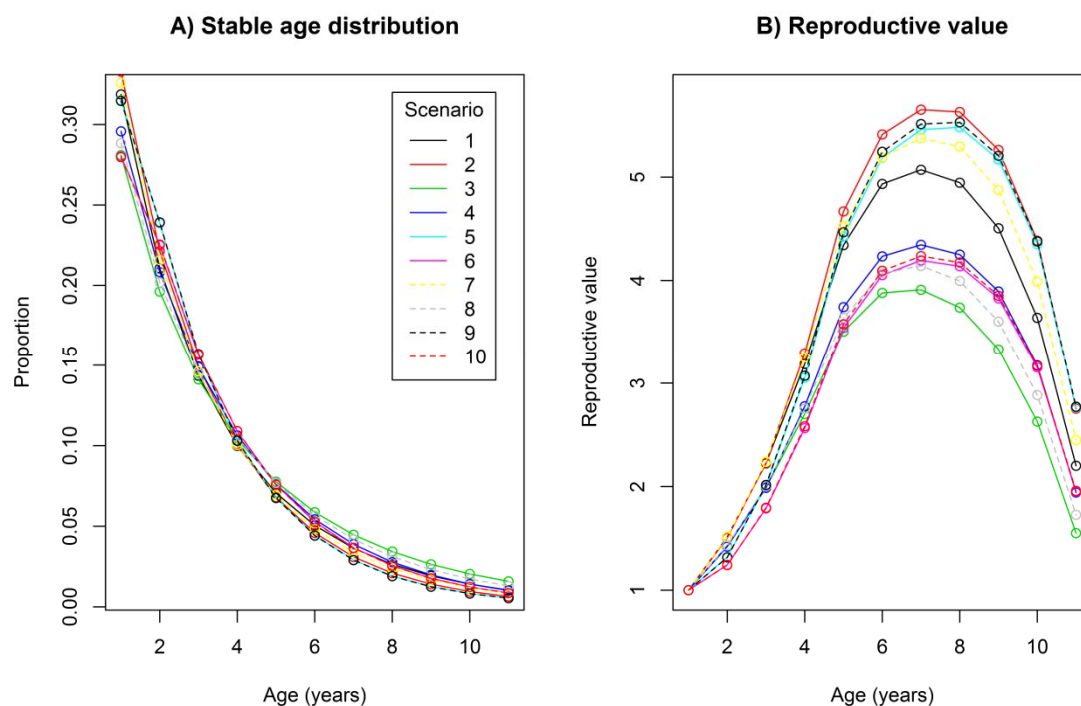


Figure 5.

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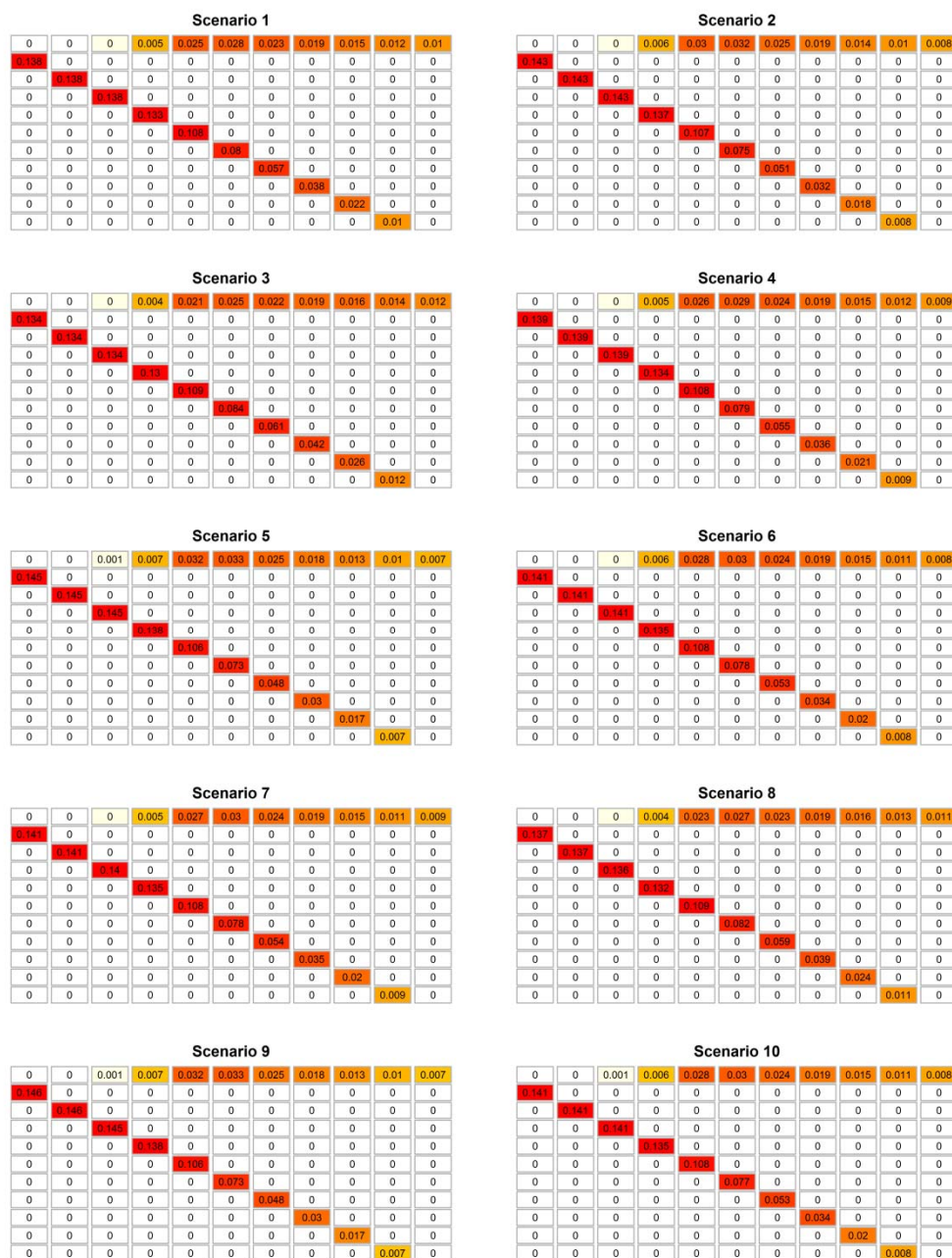


Figure 6.

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